

## **Sasakiela, a new Early Carboniferous porcelliid genus (Porcellioidea, Gastropoda) with an unusual shell ontogeny**

**Klaus Bandel**, Hamburg and **Jiří Frýda**, Prague

With 3 figures

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**Abstract:** A new porcelliid gastropod genus, *Sasakiela* gen. nov., is described from the Lower Carboniferous of Belgium. It is based on *Pleurotomaria ryckholtiana* KONINCK, 1843, and it is placed into the subfamily Agnesiinae of the Porcellioidea (Archaeogastropoda). The first two whorls of the teleoconch of *Sasakiela* are openly and planispirally coiled which suggests that juveniles of *S. ryckholtiana* (KONINCK, 1843) lived possibly within the interstices of algal thickets or reef debris like many species of the modern Caecidae. In contrast to the juveniles the adult *Sasakiela ryckholtiana* had a tightly coiled trochospiral shell and lived more exposed among the organisms of the reef environment. The distribution of openly coiled shells amongst Paleozoic gastropods is briefly discussed.

**Zusammenfassung:** *Sasakiela* stellt eine neue Gattung der porcelliid Gastropoden dar und wird aus dem Unterkarbon Belgiens beschrieben. Die Gattung basiert auf *Pleurotomaria ryckholtiana* KONINCK, 1843 und wird in die Unterfamilie Agnesiinae der Familie Porcellioidea (Archaeogastropoda) eingestuft. Die beiden ersten Windungen des Teleoconches von *Sasakiela* sind offen und planispiral aufgewunden was auf ein zwischen Algen und Geröll verborgenes Leben des Jungtieres hinweist, in etwa vergleichbar mit der Lebensweise vieler heutiger Caecidae. Im Gegensatz zu den Jungtieren lebte die erwachsene *Sasakiela ryckholtiana* mit eng gewundener trochospiraler Schale mehr im Offenen zwischen den anderen Organismen des Riffmilieus. Das Auftreten offen gewundener Gehäuse bei paläozoischen Schnecken wird angesprochen.

## Introduction

Gastropods belonging to the extinct superfamily Porcellioidea represent relatively rare elements within Paleozoic marine communities. Here an unusual change in shell coiling from dextral juvenile teleoconch to sinistral or planispiral later teleoconch represents a character, which facilitates their recognition in the fossil record. BANDEL (1993) analyzed the distribution of such unusual reversal in the mode of shell coiling amongst some Paleozoic and Mesozoic archaeogastropods. He, therefore, united the Mesozoic Cirridae with the Paleozoic Porcellidae suggesting that they represent one natural group. Accordingly members of the family Porcellidae bearing a slit during the Triassic evolved into members of the Cirridae that lacked a slit. The oldest representatives of the slit bearing Porcellidae have since been reported from Silurian strata (FRÝDA 1995, 1997). But also Paleozoic non-slit bearing species have since been discovered. The Early Devonian (Emsian) *Alaskacirrus bandeli* FRÝDA & BLODGETT, 1998 has been suggested to represent the oldest known member of the Cirridae, extending their time range considerably (FRÝDA & BLODGETT 1998). The stratigraphical range of the Porcellioidea is, thus, extended from at least the Silurian to the Late Cretaceous with the last occurrence of the genus *Hamusina* GEMMELLARO, 1878 (KIEL & BANDEL 2002). The superfamily Porcellioidea, thus, spans an interval of about 350 million years. Further research dealing with Paleozoic gastropods has revealed a relatively high morphological diversity of the Paleozoic Porcellidae. Here we report the occurrence of an unusual, new porcelliid genus that is distinguished by having an openly coiled juvenile shell. It lived in the tropical sea at Early Carboniferous time in the area, which lies nowadays in southern Belgium. Also the distribution of openly coiled shells found among Paleozoic gastropods is here briefly discussed.

All figured specimen of *Sasakiella* are deposited in the collection of the "Institute Royal des Sciences Naturelle de Belgique" in Brussels.

## Systematic paleontology

- Subclass Archaeogastropoda THIELE, 1925  
 Order Vetigastropoda SALVINI-PLAWEN, 1980

Remarks: Amongst modern marine gastropods only the Archaeogastropoda have no planktotrophic veliger larvae (BANDEL 1982) and, therefore, they never produce a true larval shell. Archaeogastropoda can be divided in two large groups, Patellogastropoda (= Docoglossa) and Vetigastropoda (= Rhipidoglossa). They are connected to each other by their early ontogeny during which only the protoconch I

(primary shell of BANDEL 1982) is formed. To their protoconch no shell is added that has been formed by a plankton feeding larva. (protoconch II). Undoubted members of the Patellogastropoda are unknown from the Paleozoic (BANDEL & GELDMACHER 1996, FRÝDA 2001). For this reason, the majority of the Paleozoic representatives of the Archaeogastropoda have tentatively been placed in the Vetigastropoda.

According to the analysis of BANDEL & FRÝDA (1996) the family-level classification of Paleozoic slit-bearing archaeogastropods used by KNIGHT et al. (1960) is of little use and may even be misleading. In addition, it also has to be taken in consideration that the diversity of the Paleozoic slit bearing archaeogastropods has been higher than today. Species with slit and selenizone in their shell probably included many groups, which are now extinct. Among Paleozoic slit-bearing Gastropoda there are not only members of the Vetigastropoda but NÜTZEL & BANDEL (2000) and BANDEL (2002) recently described Late Paleozoic genera with slit bearing shell that belong into the Caenogastropoda according to the presence of a larval shell in their protoconch. Also PAN & ERWIN (2002) illustrated such Late Permian slit-bearing gastropods with distinct caenogastropod protoconchs, but they did not recognize that they are not Archaeogastropoda. Similarly NÜTZEL & MAPES (2001) discussed a slit bearing caenogastropod from the Early Carboniferous of the USA and placed it in the archaeogastropods and even speculated about the presence of planktotrophic larvae within the archaeogastropods of that time. Such speculations are misleading if ontogeny of modern archaeogastropods is taken into consideration (BANDEL 1982). Existence of nacre and archaeogastropod-type protoconch placed the Porcellioidea clearly into the Archaeogastropoda (BANDEL 1993; YOO 1994), but their placement within the Vetigastropoda has to be considered as tentative even though it is likely.

#### Superfamily Porcellioidea KOKEN, 1895

**Diagnosis:** Gastropoda with dextral coiling in the early teleoconch whorls and sinistral or planispiral coiling in the later whorls of the teleoconch, and characteristic protoconch of the subclass Archaeogastropoda as documented by BANDEL (1982, 1993).

**Remarks:** Members of the Paleozoic family Porcellidae according to BANDEL (1993) were interpreted to have evolved during the Triassic into members of the Cirridae. For this reason BANDEL (1993) united both latter families in the superfamily Cirroidea. This systematic approach was accepted by FRÝDA (1997, 1999), FRÝDA & BLODGETT (1998), BLODGETT & FRÝDA (1999), and HEIDELBERGER (2001). Recently, we were warned by Phillipe BOUCHET (Paris) that KOKEN (1895, in ZITTEL) has to be considered as the author of the family Porcellidae and not BROILI (1924) as had been stated by KNIGHT et al. (1960). Therefore, the Porcellidae have to be regarded as the older valid family name predating the erection of the family Cirridae COSSMANN, 1916. Since rules of zoological nomenclature determine that the name of the superfamily has to be derived from the oldest family name available we have to replace the Cirroidea by the Porcellioidea, following BOUCHET's advice.

Family	Porcellidae KOKEN, 1895
Subfamily	Agnesiinae KNIGHT, 1956

Diagnosis: Porcellidae with a sinistrally coiled, trochiform teleoconch and with initial portion of shell coiling inward; selenizone narrow, situated low on whorls; ornament composed of collabral and/or spiral elements.

Discussion: KNIGHT (1956) established the subfamily Agnesiinae with no diagnosis or list of included genera. KNIGHT et al. (1960) placed the latter subfamily in the family Eotomariidae WENZ, 1938, and characterized its members as representing eotomariids with sinistral or hyperstrophic coiling. Besides the type genus *Agnesia* KONINCK, 1883, they placed the genera *Hesperiella* HOLZAPFEL, 1889 and *Enantio-stoma* KOKEN, 1896 in this subfamily. WENZ (1938) had considered these genera to belong to his Gosseletininae WENZ, 1938, of the Pleurotomariidae. KNIGHT et al. (1960) described the presence of a sinistral protoconch in some species of *Agnesia*; however, the protoconch of the type species is still unknown (KNIGHT 1941: 33). On the other hand, they described the protoconch of *Hesperiella* as coiling inwards, and they interpreted this character as suggesting hyperstrophy. YOO (1994) described and figured a juvenile shell of *Agnesia* from the Lower Carboniferous of Australia as being dextrally coiled and thus having the same shape as in *Hesperiella*. BANDEL (1993) assigned the Agnesiinae to the family Porcellidae and also added the genus *Antitrochus* WHIDBORNE, 1891 in this subfamily. Earlier, WENZ (1938) questionably had placed *Antitrochus* in the family Trochonematidae, because no slit or selenizone was observed in the type species *A. arietinus* by WHIDBORNE (1891). KNIGHT (1941), who reexamined the coarsely silicified type specimens of this species, noted also no slit and selenizone. BANDEL (1993) suggested that the Middle Devonian gastropods described as *Pleurotomaria nodulosa* SANDBERGER, 1842, and *Pleurotomaria elegans* ARCHIAC & VERNEUIL, 1842, are very similar to *Antitrochus arietinus* WHIDBORNE, 1891 and probably represent the same species. The teleoconch of *Antitrochus nodulosus* (SANDBERGER) is sinistral with a narrow selenizone at the lower edge of each whorl and with a dextrally coiled first whorl (BANDEL 1993) and, thus, it resembles *Agnesia* and *Hesperiella*. Recently, HEIDELBERGER (2001) confirmed the presence of a slit in newly analyzed specimens of the Middle Devonian *Antitrochus nodulosus* (SANDBERGER, 1842).

The oldest member of the Agnesiinae, *Pernerircirus sinistorsus* (PERNER, 1907) was reported from early Late Silurian of the Prague Basin (FRÝDA 1997). In addition, FRÝDA & BLODGETT (1998) described the unusual early shell morphology in the genus *Alaskiella* FRÝDA & BLODGETT, 1998, which is based on *Alaskiella med-fraensis* from the late Early Devonian of Alaska representing the only known species of this genus. In this species the axis of the dextrally coiled initial part of the shell is not parallel with the axis of the teleoconch, but forms an angle of about 140° with it (FRÝDA & BLODGETT 1998, pl. 1). Inclined heterostrophy was, thus, documented to occur within representatives of the Agnesiinae. This kind of heterostrophy differs from that of the Heterostropha (= Heterobranchia) where the early ontogenetic shell, usually representing the embryonic and larval shell are coiled sinistrally and the

change into dextral coiling of the teleoconch occurs just before metamorphosis or some time before it.

The recent revision of the Middle Devonian gastropod fauna of Germany has revealed two additional new genera of the Agnesiinae, *Paragnesia* BLODGETT & FRÝDA, 1999, and *Trochagnesia* HEIDELBERGER, 2001. But up to now their first whorls are not well known and their placement in the Agnesiinae, therefore, needs to be confirmed. WENZ (1938) considered the genus *Enantiostoma* KOKEN, 1896 from the Triassic to be closely related to *Agnesia*, and this position was also accepted by KNIGHT et al. (1960). But also in *Enantiostoma* the morphology of the early whorls needs to be restudied. On the other hand, protoconch morphology is known in the Triassic genus *Kokenella* KITTL, 1891, coming from Anisian to Rhaetian strata of the Alps (BANDEL 1991), Timor (KRUMBECK 1924), and Iran (NÜTZEL & SENOWBARI-DARYAN 1999). The early shell of *Kokenella* is planispirally coiled (see BANDEL 1991, pl. 2, figs. 5-7), in contrast to distinct dextral coiling in the Paleozoic Porcellinae. The latter shell character has been considered to be one of diagnostic shell features of the Porcelliidae (BANDEL 1993). Even though there is a strong similarity in teleoconch features between Triassic *Kokenella* and Late Paleozoic *Porcellia*, the taxonomic position of *Kokenella* with the Pleurotomariidae as suggested by BANDEL (1991) is considered the most likely one, since the insertion of the selenizone and its subsequent migration from apical to lateral position reflects dextral coiling in the planispiral shell. Until *Enantiostoma* is confirmed as member of the Agnesiinae there is no undoubted evidence that the members of the subfamily survived the Permian/Triassic mass extinction.

Included genera: *Pernericirrus* FRÝDA, 1997 - Silurian; *Koneprusellia* FRÝDA, 1998 - Early Devonian; *Alaskiella* FRÝDA & BLODGETT, 1998 - Early Devonian; *Paragnesia* BLODGETT & FRÝDA, 1999 - Middle Devonian; *Trochagnesia* HEIDELBERGER, 2001 - Middle Devonian; *Antitrochus* WHIDBORNE, 1891 - Middle Devonian; *Agnesia* DE KONINCK, 1883 - Devonian - Permian; *Hesperiella* HOLZAPFEL, 1889 - Devonian - Permian; *Sasakiella* gen. nov. - Early Carboniferous; *?Enantiostoma* KOKEN, 1896 - Triassic.

Genus *Sasakiella* gen. nov.

Type species: *Pleurotomaria ryckholtiana* KONINCK, 1843, from the Early Carboniferous of Belgium.

Derivatio nominis: *Sasakiella*, after the Japanese zoologist Dr. Takenori SASAKI.  
Diagnosis: Slit-bearing, low trochospiral, sinistral teleoconch, with openly coiled initial part of teleoconch; about two first whorls of teleoconch openly and planispirally coiled; protoconch being of archaeogastropod type; selenizone situated low on whorls and bearing evenly curving increments of growth (lunulae); teleoconch ornament consisting of fine collabral elements.

Discussion: The sinistrally coiled, slit-bearing teleoconch of *Sasakiella* gen. nov. resembles that of the genus *Agnesia* by several features of the shell and, thus, was placed here by KONINCK (1883, p. 100). However, *Sasakiella* differs from all known

members of the Agnesiinae by its openly and planispirally coiled juvenile teleoconch. In addition, its low trochospiral teleoconch distinguishes *Sasakiela* from the genera *Agnesia*, *Hesperiella*, *Koneprusellia*, and *Alaskiella*, all of which have medium to high-spined trochospiral teleoconchs. But also the Silurian *Pernericirrus*, and the Devonian *Paragnesia* have a low trochospiral teleoconch as is present in *Sasakiela*. However, the juvenile teleoconch of *Pernericirrus sinistorsus* (PERNER, 1903) is tightly coiled and has dextral orientation. Also its selenizone has more complex structure that differs from that of *Sasakiela*. The teleoconch of *Paragnesia costata* (GRODFUSS, 1844) has distinctly concave sides contrasting from that of *Sasakiela*.

The placement of *Sasakiela* gen. nov. into the subfamily Agnesiinae is based on the sinistral coiling of the teleoconch, position of selenizone, whorl shape and its expansion rate which are similar to those of the other members of the subfamily. The dextral coiling of the early whorls of teleoconch is one of the diagnostic characters of both subfamilies, Agnesiinae and Porcelliinae and unites them in the Porcelliidae. In *Sasakiela* the early teleoconch whorls are openly and almost planispirally coiled. The lack of distinct dextral coiling in the early shell whorls of *Sasakiela* is probably due to the development of open coiling. Thus, the lack of dextral coiling of the early shell is considered to represent a derived shell feature and *Sasakiela* can nevertheless be placed in the Agnesiinae.

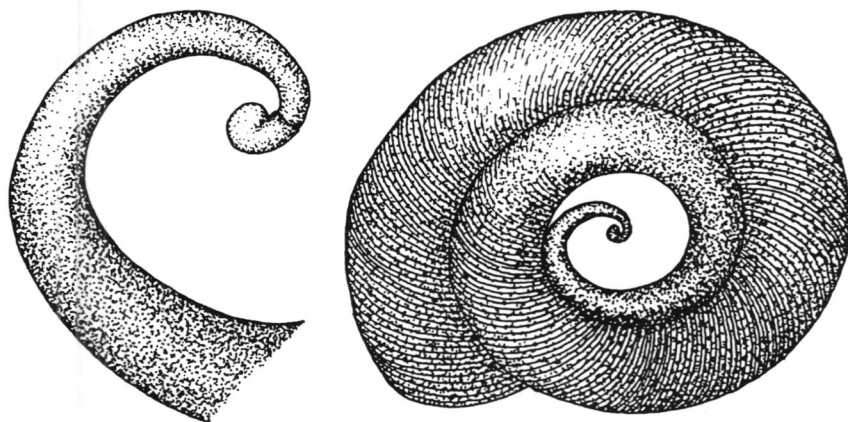
*Sasakiela ryckholtiana* (KONINCK, 1843) comb. nov.

Figs. 1-3

- 1843 *Pleurotomaria ryckholtiana*. – DE KONINCK, p. 407.  
 1843 *Pleurotomaria acuta*. – DE KONINCK, p. 400, pl. 34, fig. 6.  
 1849 *Pleurotomaria ryckholtiana*. – BRONN, p. 1018.  
 1883 *Agnesia ryckholtiana*. – DE KONINCK, p. 100, pl. 34, figs. 14-17.

The holotype is the specimen illustrated in Figs. 3.1, 3.5, 3.6 from the limestone of Visé ("assise VI" of DE KONINCK 1883). It is housed in the Museum of Natural History in Brussels, as are the illustrated paratypes.

**Description:** The small, low trochospiral teleoconch is up to 10 mm wide and sinistrally coiled. Slightly less than the two first whorls of teleoconch grew in openly and planispirally coiled mode. The apical side of the teleoconch is widely concave. Its width is about twice of the whorl width on the end of the first teleoconch whorl. The openly coiled initial part of teleoconch bears the protoconch and extends freely into the apical gape. This protoconch is of archaeogastropod type, about 0.3 mm wide, and situated slightly out of teleoconch axis (Figs. 1-3). About the first half of the teleoconch whorl is more curved than the remaining whorls, having constant translation rate. For this reason the first half of the teleoconch remained without contact to the later whorls and is openly coiled for approximately one and three quarters of revolutions. During further growth the whorl was in contact to the previous



**Fig. 1.** Drawings of *Sasakiella ryckholtiana* (KONINCK, 1843) from the Early Carboniferous of Belgium (after specimen figured here on Fig. 2.1). Detail of openly coiled initial part of its teleoconch bearing an archaeogastropod-type protoconch (left); length of protoconch about 0.3 mm. On the right an apical view onto teleoconch showing its initial part protruding into apical hollow; width of teleoconch about 6 mm.

whorl and all subsequent whorls are tightly coiled. In apical view the teleoconch shows a deviation from spiral coiling by having an elliptical outline with the longer axis of the openly coiled juvenile shell crossing a point where the whorls begin to touch each other. During later shell ontogeny, the rate of whorl translation along the shell axis increases continually and the growing shell changes its shape from planispiral to low trochospiral. The selenizone is situated low on the whorls and is covered by the subsequent whorl. It is bordered by a spiral thread on each side and is ornamented by irregularly curving spaced increments of growth (lunulae) (Figs. 2-3). The ornament of the shell consists of numerous, regularly spaced, collabral threads which are roughly as distant to each other than wide and curve backward below the suture to continue with an angle of about  $60^\circ$  with the selenizone. The basal part of the whorl is ornamented by the same type of collabral threads.

Discussion: The pseudo-elliptical outline of the teleoconch seen in apical view represents an unusual shell feature of the Archaeogastropoda and Agnesiinae (FRÝDA & MANDA 1997). The longer axis of the outlined "ellipse" in all five studied specimen runs across the point where the juvenile whorls join and represent a primary shell character. They are not a result of postmortem shell deformation.

### Discussion of openly coiled shells found among Paleozoic gastropods

The first teleoconch whorls of the Early Carboniferous *Sasakiela ryckholtiana* grew in an open coil and whorls came only into contact with each other after about two whorls had been secreted. Openly coiled shells are an unusual character found among modern as well as extinct gastropods. Modern Caecidae represent one example of such a group (BANDEL 1999). Here the process of uncoiling can be observed to effect the teleoconch as well as the larval shell of the protoconch and it differs from species to species. Also the return to normal coiling from uncoiled ancestors is documented among different species of that group.

Even though it can be studied in living gastropods, the development of free whorls during later shell stages seems to be more commonly seen in ancient and sometimes even extinct gastropod groups. YOCHELSON (1971) and PEEL (1975, 1984) noted a higher frequency of taxa with openly coiled or uncoiled whorls to occur among Paleozoic gastropods than among modern ones. They interpreted the decrease in frequency of gastropods developing free whorls as the result of an increasing predation pressure during the Phanerozoic (VERMEIJ 1987, 1993). The ecological significance of free whorl development in many Paleozoic gastropods was discussed by YOCHELSON (1971), PEEL (1975, 1984), PEEL & GUBANOV (1997), and FRÝDA et al. (2002).

**Fig. 2.** *Sasakiela ryckholtiana* (KONINCK, 1843) from the Early Carboniferous of Belgium.

**1, 6** – apical views on teleoconch showing its initial part protruding into apical hollow; **2** – apical view of another specimen; **3, 7** – apical views showing collabral ornamentation of the first teleoconch whorl of a third specimen; **4** – apical view of specimen four; **5** – detail view showing initial whorl protruding into apical hollow, specimen five. Teleoconch width: 1, 2, 6–8 mm; 3, 9.5 mm; 4, 6 mm; figure width: 5, 6.5 mm; 7, 6.2 mm.



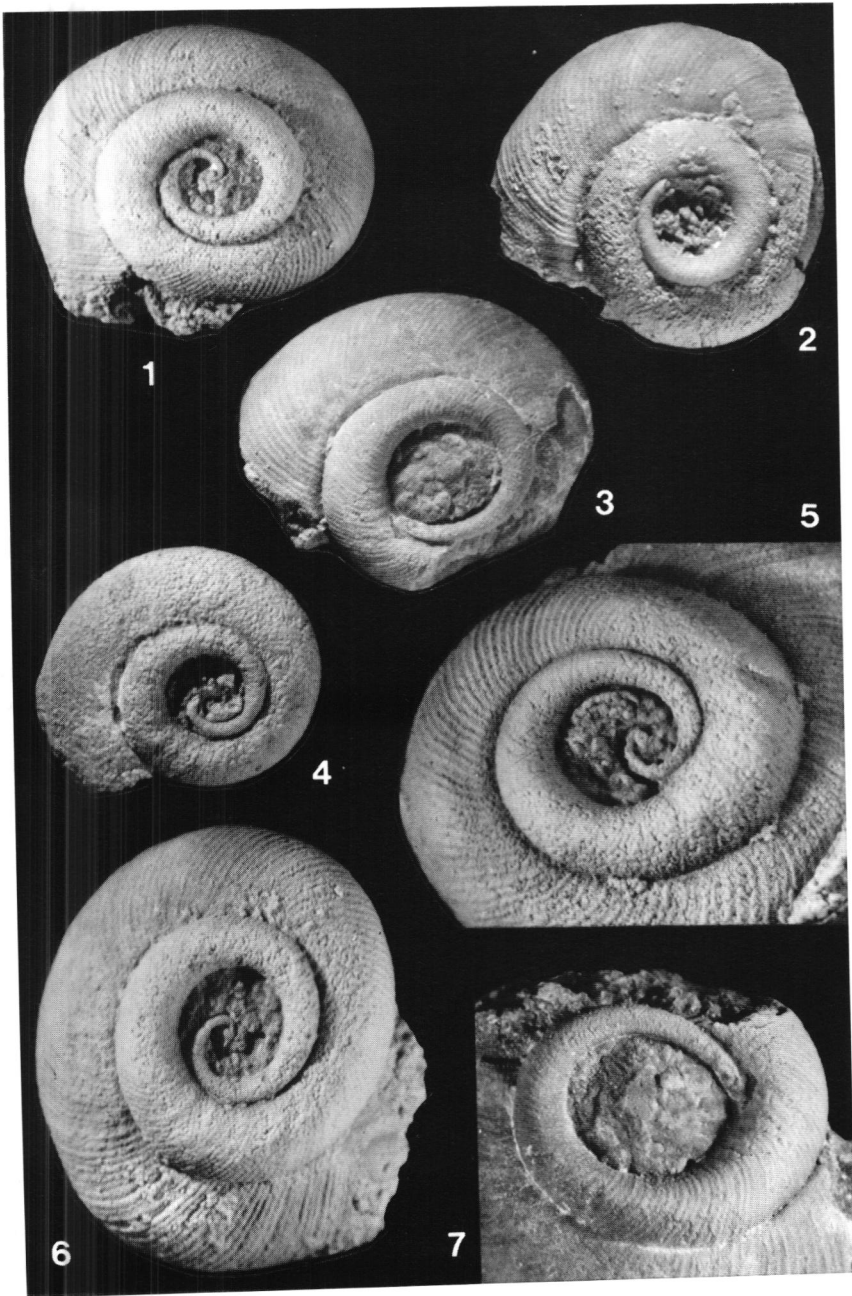
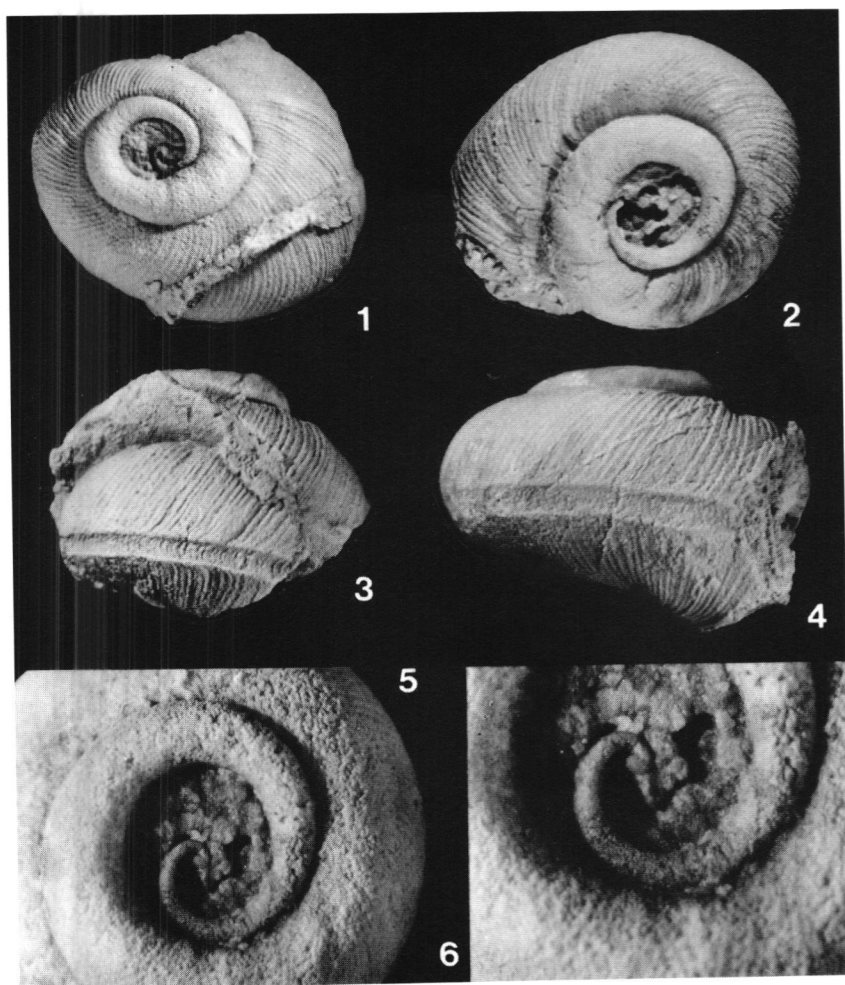


Fig. 2 (Legend see p. 142)

Devonian and Carboniferous members of the family Euomphalidae (Euomphalomorpha BANDEL & FRÝDA, 1998) such as *Serpulospira* COSSMANN, 1915, *Ecculiomphalus* PORTLOCK, 1843, *Straparollus* (*Eleutherospira*) BLODGETT & JOHNSON, 1992, and *Lytospira* KOKEN, 1896, represent typical examples of Paleozoic gastropods with free whorls. These gastropods actually have no modern counterparts since they have become extinct at the end of the Paleozoic (different view see NÜTZEL 2002). The development of a free gerontic whorl in the Silurian species *Crenilunula? markhaensis* PEEL & GUBANOV, 1997, and in the Devonian genera *Barocospira* HORNÝ, 1964, and *Ibergia* BLODGETT & FRÝDA, 1999, documents the occurrence of this shell feature among Paleozoic slit-bearing gastropods which most probably belong to the subclass Archaeogastropoda. For example the Ordovician-Silurian species of the genus *Loxoplocus* FISCHER, 1885 have disjunct, later whorls among the trochomorphs which probably also represent archaeogastropods and which detached their latest whorl from the coiled shell. WAGNER (1999) suggested independent derivations of open coiling in several genera within the Lophospiridae. Shells developing free whorls during late shell ontogeny are also known among Paleozoic gastropods belonging to the orders Cycloneritimorpha and Cyrtoneritimorpha of the subclass Neritimorpha (BANDEL & FRÝDA, 1999). The same shell feature is developed in Carboniferous species of *Helminthozyga* KNIGHT, 1930, which belongs to the subclass Caenogastropoda, order Ctenoglossa (= Ptenoglossa) (NÜTZEL 1998, pl. 30H-J). In addition, the development of an openly coiled gerontic whorl is found in some bellerophonitiform molluscs (Amphigastropoda) such as the genera *Chalarostrepsis* KNIGHT, 1948, and *Groomodiscus* ROHR & YOCHELSON, 1990. Quite unusual development of free gerontic whorls is known from members of the family Scoliostomatidae FRÝDA, BLODGETT & LENZ, 2002. In the latter gastropods, rapid growth of the inner, and later also of the basal parts of the apertural margin during their late shell ontogeny caused twisting of the gerontic whorl both outwards and backwards. This type of growth enabled a rotation of the final free whorl in an opposite direction to that of the main shell body. Thus, the gerontic aperture of these dextrally coiled shells is situated on the left side seen from the aperture.

The above-mentioned examples illustrate a development of openly coiled whorls during later shell stages. This type of deviation from tight coiling is more common than development of open coiling only in juvenile shell stages as in the case of *Sasakiella ryckholtiana*. Nevertheless, even amongst the Paleozoic gastropods such example may be found. Many species of the Devonian and Carboniferous members of the Euomphaloidea had openly coiled initial part of their teleoconchs (YOO 1994; BANDEL & FRÝDA 1998; HEIDELBERGER 2001) in the continuation of the also open and conically



**Fig. 3.** *Sasakiella ryckholtiana* (KONINCK, 1843) from the Early Carboniferous of Belgium.

**1, 3** – apical and lateral views showing collabrat ornamentation and selenizone, specimen five; **2, 4** – apical and lateral views, specimen six; **5, 6** – detail views on openly coiled initial part of teleoconch bearing an archaeogastropod-type protoconch, holotype. Teleoconch width: 1, 3 – 9 mm, 3, 4 – 8 mm; figure width: 5 – 4.2 mm, 6 – 3.5 mm.

rounded embryonic shell. Similarly the Ordovician-Permian gastropods united to the Cyrtoneritimorpha BANDEL & FRÝDA, 1998 had an openly coiled first whorl. In contrast to the Euomphaloidea, this openly coiled protoconch of the Cyrtoneritimorpha represented with exception of the small embryonic initial shell cup a true larval shell that probably formed while the veliger larva lived in and from the plankton. Openly coiled larval shells are also known in the members of the Peruneloidea FRÝDA & BANDEL, 1997, which have been interpreted to represent the basal or ancestral group of the Caenogastropoda (BANDEL 1997; FRÝDA 1998, 1999, 2001; FRÝDA & BANDEL 1997; FRÝDA & MANDA 1997; NÜTZEL et al. 2000) or related but independent groups to the caenogastropods (BANDEL 2002). Thus, in the two latter groups, Cyrtoneritimorpha and Peruneloidea, the openly coiled whorl is restricted to the protoconch whorl, and does not represent the juvenile teleoconch as is the case in *Sasakiella ryckholtiana*.

### **Interpretation of the function of uncoiling of the early shell of *Sasakiella ryckholtiana***

The early teleoconch of the Early Carboniferous *Sasakiella ryckholtiana* is openly coiled similarly to that of many species of the Euomphaloidea. But in contrast to the latter its embryonic shell was twisted into the spiral, as is characteristic to archaeogastropods. LINSLEY & YOCHELSON (1973) analyzed the shell morphology of some Devonian euomphalids from Europe and North America and speculated on their life strategy. They came to the conclusion that the Middle Devonian euomphalids have led a sedentary life. Shells of other organisms are often found attached to their shells, and they may have had limited selection pressures exerted by predators (LINSLEY & YOCHELSON 1973). They also suggested that the carrying position of medium-sized, low-spired shells as that of *Straparollus* was difficult to balance on the foot and crawling about seemed to be improbable and such euomphalids probably mostly rested on the bottom of the sea leading a sedentary life (LINSLEY & YOCHELSON 1973, fig. 3). A similar life position of shells was suggested by FRÝDA (1997) interpreting the ecology of the oldest porcelliids which have a large, flattened, discoidal shell. On the other hand, development of shells with high spire and the reduction of the shell size in post-Silurian Agnesiinae was interpreted as reaction to a higher mobility of these forms (FRÝDA 1997).

The juvenile teleoconch of *Sasakiella ryckholtiana* with two whorls had a ring-like shape. The inner diameter of the apical hollow in such a juvenile shell is much wider than whorl width (Fig. 3-5, 6). Such a shape of the early teleoconch had a center of gravity very far from the shell aperture. At this stage of shell growth *Sasakiella ryckholtiana* probably did not carry its shell

balanced on the foot but held it up, since it was small and light. The shell of *Sasakiela ryckholtiana* was relatively small, in contrast to that of adult euomphalids, which had probably their shells mostly rested on the bottom. But juvenile euomphalids may have lives in a rather similar way as *Sasakiela*, until they began coiling tightly or grew to larger size becoming heavier. The open coiled juvenile shell allows a comparison of the mode of life in *Sasakiela ryckholtiana* with that of living Caecidae (BANDEL 1999), which live protected in interstices.

As shown by LINSLEY (1977, 1978) the development of openly coiled whorls during late ontogeny of the gastropod shells is typically connected with a change from more mobile to sessile style of life. The change seen in *Sasakiela ryckholtiana* is from openly to closely coiled teleoconch whorls instead. In early life ranging from metamorphosis to more fully grown existence after the embryonic stage to about the time when two whorls of the teleoconch were completed, *Sasakiela ryckholtiana* probably carried its shell upright and lived among algae, or animal produced thickets, or within the interstices of reef rubble, quite similar to modern representatives of the Caecidae. Its radial aperture also supports such an interpretation. Subsequent development of the closely coiled, trochomorph teleoconch may have enabled to carry the shell in normal gastropod manner. Thus, the adult *Sasakiela ryckholtiana* may be seen as mobile snail moving about among the organisms within the reef environment or among the rubble of the reef. The rock type from which *S. ryckholtiana* was extracted presents evidence for a life among coral and bryozoan colonies in tropical shallow water environment. But it has to be taken into consideration that the possibilities of interpretation of shell shape and mode and place of life are limited, as was documented in case of the modern gastropods that live in the shallow sea and coastal environment of the Caribbean Sea of Columbia. Here the analysis carried out by BANDEL & WEDLER (1987) indicated that with only few exceptions shell shape appears to be more a matter of systematic place of its carrier than its ecology. But commonly juvenile individuals of a gastropod species lead a more secluded life and have a quite different shell shape than fully grown and larger individuals, as can be noted for example in case of *Cypraea* and *Strombus* among others.

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#### Addresses of the authors:

Prof. Dr. KLAUS BANDEL, Universität Hamburg, Geologisch-Paläontologisches Institut und Museum, Bundesstraße 55; D-20146 Hamburg, Germany.  
E-mail: bandel@geowiss.uni-hamburg.de

RNDr. JIŘÍ FRÝDA, Dr, Czech Geological Survey, Klárov 3/131; CS-11821 Praha 1, Czech Republic.  
E-mail: fryda@cgu.cz